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Rasmussen, Jan Audun Liljeroth; Surlyk, Finn

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JAN AUDUN RASMUSSEN & FINN SURLYK

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Coiled nautiloid cephalopods of the genus *Discoceras* are locally common in the Middle and Upper Ordovician of Baltica, for example in the Oslo Graben, but are exceedingly rare in contemporaneous strata from the Danish island of Bornholm. The two new species of *Discoceras* described here, *D. costatum* n. sp. and *D. vasegaardense* n. sp., occur in shales of the Upper Ordovician Lindegård Formation. The nautiloids are preserved as external molds in laminated siliciclastic mudstones. The very rare occurrence of cephalopods, combined with the apparently endemic nature of the *Discoceras* fauna, may be explained by the location of Bornholm distally on the Baltoscandian shelf combined with the influence of relatively cold ocean currents from the adjacent Rheic Ocean.

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Jan Audun Rasmussen [janr@snm.ku.dk], Natural History Museum of Denmark, University of Copenhagen, Øster Voldgade 5–7, DK-1350 Copenhagen K, Denmark.
Finn Surlyk [finns@geo.ku.dk], Department of Geography and Geology, University of Copenhagen, Øster Voldgade 10, DK-1350 Copenhagen K, Denmark.

Coiled nautiloid cephalopods are exceptionally rare in the Lower Palaeozoic shales of the island of Bornholm, Denmark, located in the Baltic Sea south of Sweden. They have not been described or figured earlier, but the tarphycerid genus *Discoceras* was noted to occur within the Upper Ordovician Lindegård Formation, formerly referred to as the *Tretaspis* shale (C. Poulsen 1964; V. Poulsen 1966). In contrast they are relatively common in the Middle and Upper Ordovician of Baltica, for example in the Oslo Graben in Norway and in Estonia (e.g. Sweet 1958). A loose specimen here referred to the genus *Discoceras* was recently found on the beach at Sose Bugt east of Sose Odde on the south coast of Bornholm (Fig. 1). Together with two coiled nautiloids from the collections in the Natural History Museum of Denmark (SNM) it makes up a total of three specimens of coiled nautiloids from the Upper Ordovician succession of Denmark known so far. Slabs of the lower Upper Ordovician *Dicellograptus* shale are very common on the beach at Sose Bugt and contain abundant specimens of diplograptid graptolites. Pieces of the upper Upper Ordovician Lindegård Formation occur as well, but less commonly. Most likely, the major part of the Lindegård Formation slabs originates from the area between Sose Bugt and the rivulet Øleå some 10 km towards the southeast. The aim of this paper is to describe the tarphycerid nautiloids from Bornholm and to place them into the context of other finds of *Discoceras* from correlative successions elsewhere on Baltica.

Stratigraphy

The Upper Ordovician succession of Bornholm comprises the *c.* 21 m thick *Dicellograptus* shale (Pedersen 1989; Schovsbo *et al.* 2011) and the overlying more than 20 m thick Lindegård Formation (Pedersen 1989, fig. 12), the latter unit including the Jerrestad Formation and Tommarp Mudstone of Pedersen (1989) (Fig. 2). The *Dicellograptus* shale consists of black and dark grey, organic-rich, graptolite-bearing laminated mudstone usually showing a distinct shaly parting (Pedersen 1989), whereas the Lindegård Formation typically consists of more massive, grey or brownish

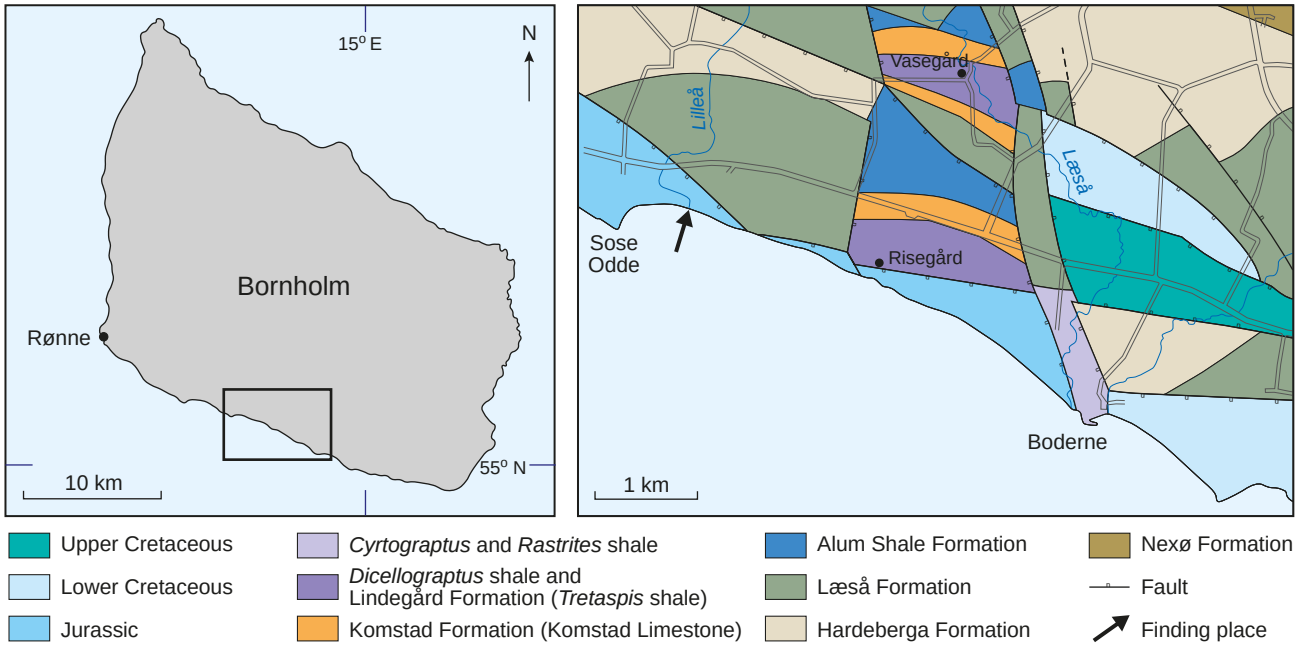

Fig. 1. Geological sketch map showing the two Bornholm localities where *Discoceras vasegaardense* n. sp. and *D. costatum* n. sp. were found. The arrow east of Sose Odde indicates where the *D. vasegaardense* n. sp. specimen (MGUH 29286) from Sose Bugt was found loose on the beach. *D. costatum* n. sp. (MGUH 29285) and most likely also the holotype of *D. vasegaardense* (MGUH 29287) were collected next to Vasegård (also spelled Vasegaard). The map is modified from H. Gry after Poulsen (1969), including the lithostratigraphic revisions by Nielsen & Schovsbo (2007).

mudstone and occasionally siltstone containing a benthic fauna, including trilobites and brachiopods (Ravn 1899; Kielan 1959).

The *Dicellograptus* shale has been correlated with parts of the Sularp, Skagen, Mossen and Fjäcka Formations in Sweden (e.g. Bergström *et al*. 1999; Pålsson 2001), but these subdivisions cannot easily be recognised on Bornholm. Accordingly, the old, informal name is maintained here, awaiting a lithostratigraphical revision of the unit. The upper 10 m of the *Dicellograptus* shale of Bornholm crops out at the Læså and Risebæk rivulets, where it comprises the *Diplograptus foliaceus*, *Dicranograptus clingani* and *Pleurograptus linearis* graptolite zones (Bruvo & Nielsen 2004). At the Risebæk locality, which is situated next to the farm Risegård (Fig. 1), conodonts from a limestone nodule 3 m below the top of the *Dicellograptus* shale belong to the upper part of the *Amorphognathus superbus* conodont Zone (Stouge & Rasmussen 1996). The overlying Lindegård Formation, established by Glimberg (1961) in Skåne, Sweden, corresponds to the *Trinucleus* shale (Gry 1948; C. Poulsen 1936), the *Tretaspis* shale (V. Poulsen 1966, 1968, 1969), and the Jerrestad Formation and Tommarp Mudstone (Bergström 1982; Pedersen 1989; Schovsbo *et al*. 2011). The lowermost part of the Lindegård Formation correlates with the Upper Ordovician *Dicellograptus complanatus* graptolite Zone and the overlying part includes the Upper Ordovician *Staurocephalus clavifrons*, *Eodindymene pulchra*, *Dalmanitina olini*, *Dalmanitina mucronata* and *Brongniartella platynota* trilobite zones (V. Poulsen 1966), which correlate with the *Dicellograptus anceps*, *Normalograptus extraordinarius* and *N. persculptus* graptolite zones (see Chen *et al*. 2006).

Chronostratigraphy			Graptolite zones	Litho-stratigraphy Bornholm
System	Global stages	British Series		
Bergström *et al*. (2009)			Chen *et al*. (2006) Bruvo & Nielsen (2004)	Schovsbo *et al*. (2011)
Upper Ordovician	Hirnantian	Ashgill	*N. persculptus* / *N. extraordinarius*	Lindegård Fm.
	Katian		*D. anceps* / *D. complanatus*	
		Caradoc	*P. linearis* / *D. clingani*	*Dicellograptus* shale
	Sandbian		*D. foliaceus* / *N. gracilis*	

Fig. 2. Stratigraphy of the Upper Ordovician strata from the island of Bornholm, Denmark. Grey filling represents depositional hiatus.

Two of the three nautiloid-bearing shale samples contain additional benthic fossils. A brachiopod belonging to the superfamily Plectambonitoidea of the order Strophomenida was observed in the shale slab containing cephalopod specimen MGUH 29286 (determined by David A.T. Harper, 2011), whereas the slab containing specimen MGUH 29287 shows two imprints of the trilobite *Tretaspis* (determined by Arne T. Nielsen, 2011). These findings together with the lithological characteristics of the three slabs indicate that they all originate from the Lindegård Formation rather than the *Dicellograptus* shale.

Palaeobiogeographic significance

The two new species of *Discoceras* from Bornholm are not known with certainty from other regions. *Discoceras antiquissimum*, which resembles *D. costatum* n. sp. is known from several Baltoscandian localities, including the Upper Ordovician Nabala, Vormsi and Pirgu Stages (formerly "Lyckholm-Stufe") of northern Estonia (Eichwald 1842; Teichert 1930) and the Upper Ordovician Husbergøya Formation (formerly 5a) of the Oslo Region, Norway (Strand 1933). In addition it has been described from probably Upper Ordovician erratic boulders of Zawidowice, southern Poland (Roemer 1861; Dzik 1984).

Discoceras vasegaardense n. sp. is similar to, but not identical with, a Darriwilian to lower Sandbian species of *Discoceras*, which commonly has been named *Discoceras arcuatum* (Lossen), but this name is regarded as a *nomen nudum* herein (see Systematic palaeontology below). "*D. arcuatum*" is known from the uppermost part of the Elnes Formation in the Oslo Region, Norway (Lossen 1860; Sweet 1958). Hence, the two Bornholm species are undoubtedly related to relatively shallow water species of *Discoceras* that are common in more proximal parts of the Baltic platform, but are different from these at the species level.

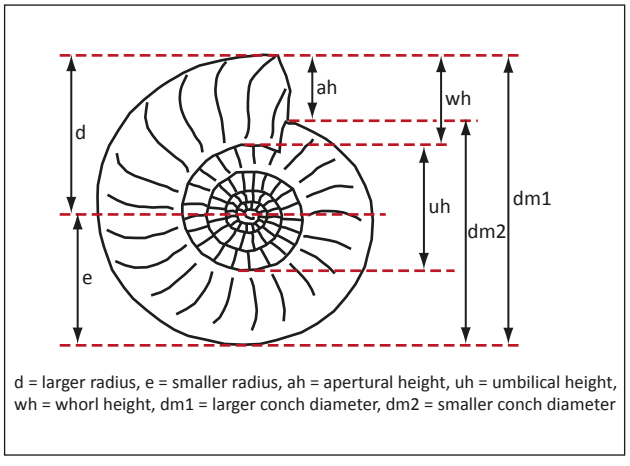

Fig. 3. Principal descriptive conch characters used in the present study (modified from Korn & Klug 2003).

The very rare occurrence and the apparently endemic nature of the Late Ordovician *Discoceras* fauna from Bornholm may probably be explained by the distal shelf palaeoenvironment on the southern margin of Baltica combined with influence of temperate to boreal ocean currents from the adjacent Rheic Ocean (Dzik 1983; Christiansen & Stouge 1999).

Systematic palaeontology

Class Cephalopoda Cuvier, 1797
Subclass Nautiloidea Agassiz, 1847
Order Tarphycerida Flower & Kummel, 1950
Family Discoceratidae Dzik, 1984
Genus *Discoceras* Barrande, 1867

Type species: *Clymenia antiquissima* Eichwald, 1842, from the Katian Stage, Upper Ordovician, Estonia.

Diagnosis (after Furnish & Glenister 1964, p. K360): Gradually expanded ribbed or smooth forms characterized by slight to moderate impression and subquadrate whorl section; siphuncle central in initial half-volution, marginodorsal in succeeding 1.5–2 whorls, subdorsal at maturity; connecting rings thick, layered. Upper Ordovician, Llandeilo–Ashgill.

Remarks: *Schroederoceras* Hyatt, 1894 is regarded as a junior synonym of *Discoceras* (Strand 1933; Furnish & Glenister 1964). All figured specimens are housed in the type collections of the Natural History Museum of Denmark (Geological Museum; MGUH).

Characters and indices related to the shape of the shell (Fig. 3) have been described according to the suggestions by Korn & Klug (2003) used for description of coiled ammonoids.

Discoceras costatum n. sp.

Fig. 4A–B
aff. 1842 *Clymenia antiquissima* Eichwald – Eichwald, pp. 33–35, pl. 3, figs 16, 17.
aff. 1861 *Lituites antiquissimus* (Eichwald) – Roemer, pp. 62–65, pl. 6, fig. 2f (*partim*), not pl. 6, figs 2a–2e, 2g.
aff. 1925 *Discoceras antiquissimum* (Eichwald) – Foerste, pp. 58–59, pl. 18, figs 1A, 1B [copy of holotype figured by Eichwald (1842)].
aff. 1933 *Discoceras antiquissimum* (Eichwald) – Strand, pp. 33–36, pl. 2, figs 4, 11; pl. 4, figs 2, 3; pl. 13, fig. 9 (with additional synonymy).

aff. 1953 *Discoceras antiquissimum* (Eichwald) – Balashov, pp. 265–266, pl. 4, figs 2a, 2b; pl. 9, fig. 3; pl. 12, fig. 1a, b [copy of holotype figured by Eichwald (1842)].
aff. 1958 *Discoceras antiquissimum* (Eichwald) – Sweet, pl. 11, figs 1, 2.
aff. 1984 *Discoceras antiquissimum* (Eichwald) – Dzik, text-fig. 9c–d, pl. 7, fig. 1a–b.

Holotype: The holotype is a fragmented, external mold (MGUH 29285) kept in the Palaeozoic collections of the Natural History Museum of Denmark.

Type locality: The holotype MGUH 29285 was collected from shale exposures at the farm Vasegård, Åkirkeby, Bornholm (UTM zone 33U, 492789E 6100883N, datum WGS 84).

Type stratum: Lower part of the Lindegård Formation, upper Katian, Upper Ordovician.

Derivation of name: The species name *costatum* refers to the characteristic transverse ribs (from Latin: costae).

Material: One specimen (accession number 1984.455; MGUH 29285) from the Palaeozoic collections of the Natural History Museum of Denmark collected at the farm Vasegård, Bornholm.

Diagnosis: A moderately expanding *Discoceras* with a sculpture consisting of transverse, prominent ribs, usually irregularly spaced. Approximately 30 ribs are visible in the outer whorl. Whorl expansion rate (WER = $(dm1/dm2)^2$) is 2.14. Between five and fifteen secondary, transverse lirae are situated between the ribs.

Description: The holotype (Fig. 4, MGUH 29285) is a fragmented, flattened, coiled, convolute phragmocone with a diameter of 79 mm and almost 2½ volutions preserved. The living chamber is missing. The height of the last whorl (wh) is 25 mm, and the umbilical height (uh) is 35 mm (see Fig. 3 for explanation). The whorl expansion rate (WER) is 2.14, meaning that the conch is moderately expanding (see Fig. 3). Cross section of conch and internal characters are not preserved, but the imprint zone, which is the difference between wh and the apertural height (ah), is narrow as judged from the side view. Ornamentation consists of approximately 30 transverse, oblique, sharp, prominent ribs per whorl, usually irregularly spaced. Ribs form a distinct hyponomic sinus. Between 5 and 15 (on average *c.* 10) secondary, transverse lirae (growth lines) are situated between the ribs. Bifurcated lirae occur sporadically. The overall morphology of the shell is characterised as mimosphinctid according to the scheme of Korn & Klug (2003, fig. 3).

Remarks: *Discoceras costatum* n. sp. shares characters with one of the earliest species of *Discoceras*, the upper Darriwilian to Sandbian *D. boreale* Sweet, 1958, and two younger species, the Katian *D. antiquissimum* (Eichwald, 1840), and the Hirnantian *D. siljanense* Kröger, Ebbestad, Högström & Frisk, 2011. The three species are characterised by prominent transverse ribs and distinct lirae similar to those of *D. costatum*. The latter specimen differs, however, from *D. siljanense* in having fewer ribs per whorl (*c.* 30 instead of *c.* 40), and a higher whorl expansion rate (WER 2.14 instead of 1.82). It differs from *D. boreale* Sweet in having significantly fewer ribs (*D. boreale* has more than 50 per whorl; see holotype figured by Sweet 1958, pl. 9, fig 1).

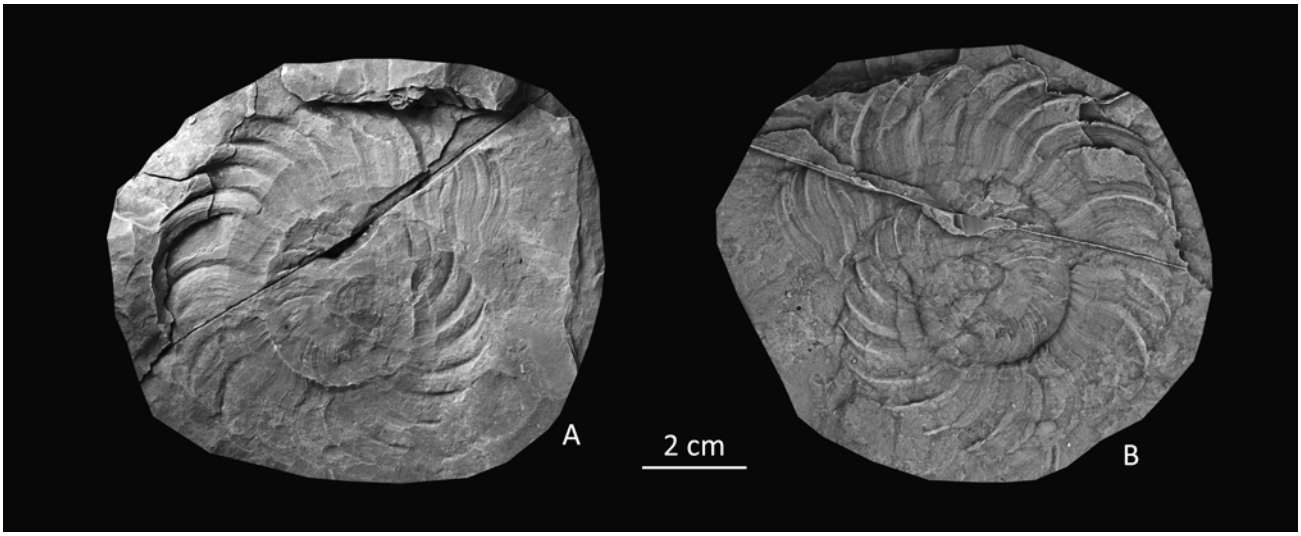

Fig. 4. *Discoceras costatum* n. sp. from the Lindegård Formation of Vasegaard, Bornholm. **A**, lateral view of specimen MGUH 29285. **B**, latex cast of A.

D. antiquissimum is characterised by almost the same number of ribs per whorl as *D. costatum* (*c.* 30–38 *vs. c.* 30), but the ribs are generally less curved and characterised by a more shallow hyponomic sinus (see description by Strand, 1933). The whorl expansion rate (WER) is higher in *D. costatum* (2.14) than in *D. antiquissimum* (between 1.65 and 2.07; 1.65 in the holotype).

Occurrence: *D. costatum* n. sp. is only known from the Upper Ordovician Lindegård Formation of Bornholm. The closely related species *Discoceras antiquissimum* is known from Katian (Upper Ordovician) strata in northern Estonia, the Oslo Region in Norway, and Sweden.

Discoceras vasegaardense n. sp.

Fig. 5A–D

aff. 1860 *Lituites arcuatus* n. sp. – Lossen, pp. 25 [*nomen nudum*].

aff. 1861 *Lituites antiquissimus* (Eichwald) – Roemer, pp. 62–65, pl. 6, figs 2b, c (*partim*).

aff. 1933 *Discoceras angulatum* (Saemann) – Strand, pp. 37–38, pl. 2, fig. 3; pl. 4, fig. 4 (picture and description of the holotype figured by Saemann 1852).

aff. 1953 *Schroederoceras angulatum* (Saemann) – Balashov, pp. 263–264, pl. 13, figs 1a, 1b, 2a, 2b.

aff. 1953 *Schroederoceras spongistratum* n. sp. – Balashov, pp. 254–255, pl. 7, fig. 8; pl. 8, figs 1, 2; pl. 9, fig. 3.

aff. 1958 *Discoceras arctuatum* [sic] (Lossen) – Sweet, pp. 103–104; textfig. 13J; pl. 12, fig. 4, ?pl. 8, fig. 7.

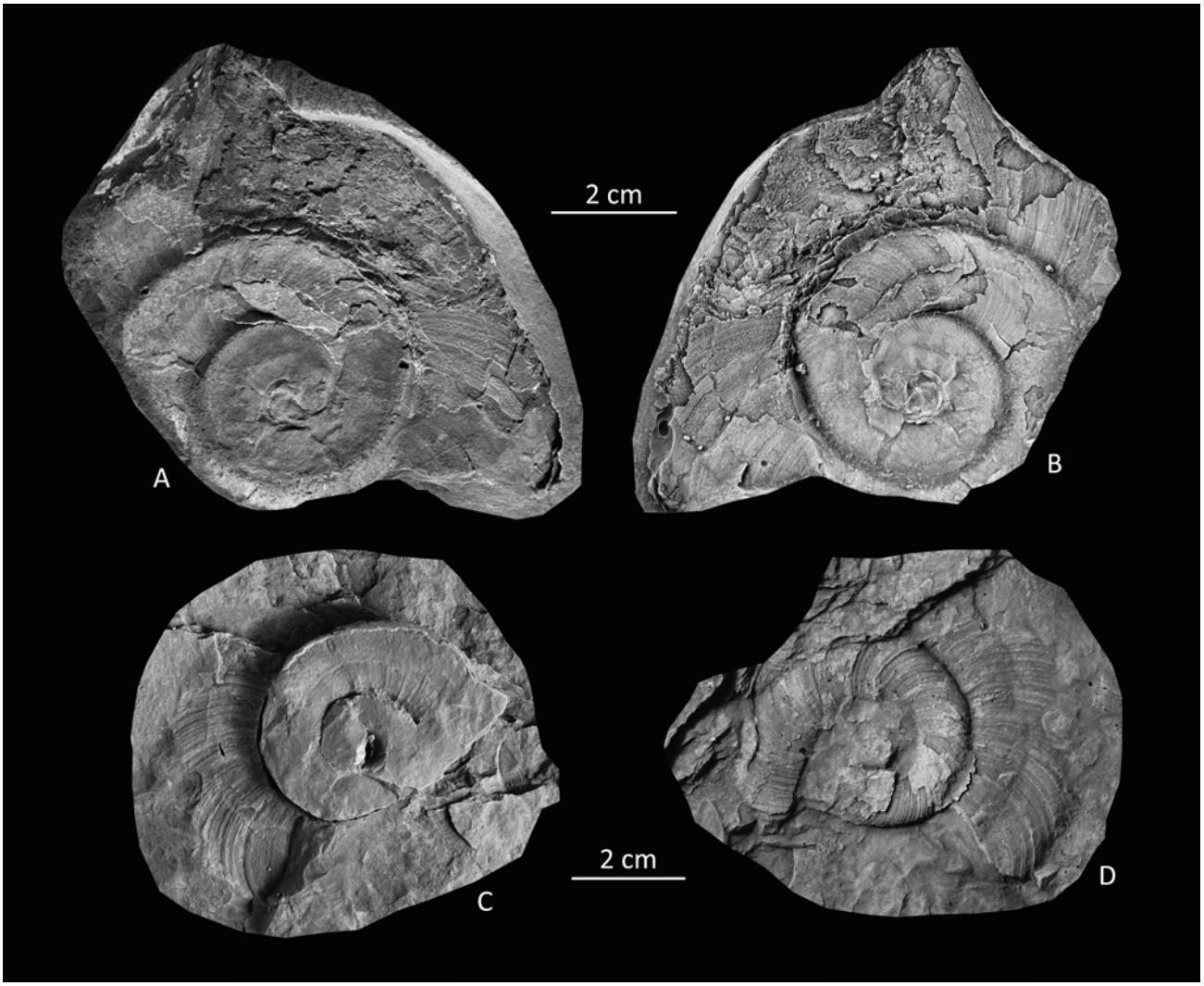

Fig. 5. *Discoceras vasegaardense* n.sp. from the Lindegård Formation of Bornholm. **A**, lateral view of specimen MGUH 29286 from a loose slab from the beach at Sose Bugt. **B**, latex cast of A. **C**, lateral view of specimen MGUH 29287, presumably found close to the farm Vasegård near the town Åkirkeby, Bornholm. **D**, latex cast of C.

Comments on the synonymy: *Lituites arcuatus* Lossen, 1860 was originally established on the basis of two specimens from the uppermost part of the Elnes Formation (previously named the Cephalopod shale) of Toten in the northern part of the Oslo Region, Norway, which has been dated as lower Sandbian (*N. gracilis* Zone). One specimen was from the village Billerud. Lossen did not illustrate the specimens and they were probably lost during the Second World War. According to Sweet (1958) one of the specimens was illustrated and described by Strand (unpublished notes, Oslo University) during a visit to Museum für Naturkunde, Berlin, before the war. Sweet (1958) diagnosed, described and illustrated the species based on the notes by Strand but he did not select a neotype for *Lituites arcuatus*. Accordingly, "*Lituites arcuatus*" is recognized as a *nomen nudum*.

Holotype: The holotype is a fragmented, external mold (MGUH 29287) kept in the Palaeozoic collections of the Natural History Museum of Denmark.

Type locality: The original label associated with the holotype MGUH 29287 says "Vasegaard?", indicating that the specimen likely originates from exposures next to the farm Vasegård near Åkirkeby, Bornholm (UTM zone 33U, 492789E 6100883N, datum WGS 84).

Type stratum: Lindegård Formation, upper Katian, Upper Ordovician.

Derivation of name: The specific name *vasegaardense* refers to the type locality, which presumably is situated near the farm Vasegård, Bornholm.

Material: Two specimens. MGUH 29286 is from an erratic shale slab found by Tom Christensen on the beach at Sose Bugt, Bornholm (approximately at UTM 489690E/6099554N), surrounded by numerous pieces of loose Upper Ordovician shales. MGUH 29287 (holotype) is from the Palaeozoic collections of the Natural History Museum of Denmark. The finder is unknown, but according to the label the specimen originates from the *Tretaspis* shale (Lindegård Formation) presumably at the farm Vasegård, Bornholm.

Diagnosis: Moderately to strongly expanding *Discoceras* with a smooth surface except for distinct, closely spaced, transverse lirae (growth lines). The whorl expansion rate (WER) varies between 2.39 and 2.43 and the umbilical width index UWI = uh/dm1 is between 0.46 and 0.50 (see Fig. 3 for explanation of the individual characters).

Description: The two specimens are both fragmented and flattened. The conch consists of coiled, convolute phragmocones with diameters of *c.* 85 mm in MGUH 29286 (Fig. 5A–B) and 55 mm in MGUH 29287 (Fig. 5C–D). Almost 2½ volutions are preserved in both specimens, and the living chamber is missing. The height of the last whorl (wh) is 18 mm in MGUH 29286 and 12 mm in MGUH 29287, and the umbilical heights (uh) are 40 mm and 30 mm, respectively. The conch is moderately to strongly expanding. The whorl expansion rate (WER) varies between 2.39 and 2.43 and the umbilical width index (UWI) varies between 0.46 and 0.50 judging from the most well-preserved parts of the phragmocone (see Fig. 3 for explanation of the individual characters).

Cross section of conch and internal characters are not preserved. The outer surface of the conch is almost smooth except for distinct, closely packed, slightly curved lirae (growth lines) that are occasionally bifurcated. A longitudinal, narrow, centrally placed impressed zone is seen in the second and third volutions. The overall morphology of the shell may be characterised as transitional between mimosphinctid and convoluticeratid according to the scheme of Korn & Klug (2003, fig. 3).

Remarks: *Discoceras vasegaardense* resembles "*Discoceras arcuatum* (Lossen)" (*nomen nudum*) in many aspects, but its whorl expansion rate (WER) is clearly higher. In *D. vasegaardense* it varies between 2.39 and 2.43, while it is 1.90–2.25 in "*D. arcuatum*". In "*D. arcuatum*" figured by Sweet (1958, pl. 12, fig. 4), which is a photograph of one of the two original, now lost, specimens described by Lossen (1860), WER is 2.2. Measurements of WER in specimens of *Discoceras angulatum* figured by Strand (1933, pl. 4, fig. 4; holotype) and Balashov (1953, pl. 13, fig. 1) show that also this species is characterised by a clearly lower WER than *D. vasegaardense* (1.9 *vs.* 2.39–2.43) despite the overall similarity. The same tendency is seen in *D. spongistratum* (Balashov, 1953) where WER = 2.1 (see Balashov 1953, pl. 8, fig. 1).

The holotype of *D. vasegaardense* (MGUH 29287) was identified as a *Discoceras* species in a lecture by Christian Poulsen in 1963 (Poulsen 1964), but he never described or figured the specimen.

Occurrence: *Discoceras vasegaardense* has only been documented from the Upper Ordovician shales of the Lindegård Formation on Bornholm. The closely related species "*Discoceras arcuatum* (Lossen)" (*nomen nudum*) resembles *Discoceras vasegaardense* and may be a possible ancestor to this. "*D. arcuatum*" is known from upper Middle and lowermost Upper Ordovician strata in the Oslo Region, Norway (Lossen 1860, Sweet 1958).

Acknowledgements

Specimen MGUH 29286 of *Discoceras vasegaardense* n. sp. was found by amateur palaeontologist Tom Christensen. It was donated to Jens Kofoed from Natur-Bornholm who forwarded it to FS. Björn Kröger and Per Ahlberg are sincerely thanked for reviewing the manuscript and offering many helpful suggestions. We are thankful to Sten Lennart Jacobsen who made latex casts and photographed the specimens, and to Jette Halskov for drafting. Arne T. Nielsen is thanked for discussion and valuable comments on an earlier draft of the manuscript. We are grateful for trilobite and brachiopod identifications by Arne T. Nielsen and David Harper. Funding by the Carlsberg Foundation to JAR in support of Ordovician cephalopod studies is gratefully acknowledged.

Dansk sammendrag

Spiralsnoede, nautiloide cephalopoder tilhørende slægten *Discoceras* er yderst sjældne i Mellem og Øvre Ordovicium på Bornholm, men er almindeligt forekommende på Balticakontinentet, fx i Oslo-området og i Estland. Til dato er kun tre eksemplarer kendt fra Danmark. De stammer alle fra Lindegård Formations skiferaflejringer fra Øvre Ordovicium på Bornholm og tilhører de to nye arter *Discoceras costatum* n. sp. og *Discoceras vasegaardense* n. sp. Nautiloiderne er bevaret som ydre aftryk. Den meget sjældne forekomst af nautiloide blæksprutter generelt og *Discoceras* især, skyldes formentlig den distale placering af Bornholm på den baltoskandiske kontinentalsokkel kombineret med påvirkninger af relativt kolde havstrømme fra det Rheiske Ocean igennem Sen Ordovicium.

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